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THE

AMERICAN NATURALIST

VOL. XXIX. February, 1895. 338

THE PHILOSOPHY OF FLOWER SEASONS, AND THE PHAENOLOGICAL RELATIONS OF THE ENTOMOPHILOUS FLORA AND THE ANTHOPHILOUS INSECT FAUNA.

BY CHARLES ROBERTSON.

The writer's determination to discuss the subject of flower seasons at the present time is owing to the publication, by Mr. Henry L. Clarke, of an interesting and suggestive paper on the same topic in the NATURALIST for September, 1893. Having been engaged since 1886 in the investigation of the mutual relations of flowers and insects, he has been led in a very natural way to consider the time of blooming of flowers adapted to insects and the time of flight of the insects which depend more or less upon a floral diet. In 1890 a tabulation of both groups was begun, based upon the data then at hand, and since that time the author has had lying before him lines indicating the periods of the separate species and curves indicating the periods of the families of entomophilous plants and of the genera of bees, and the families of the principal remaining anthophilous insects; all, however, in the process of being modified by the accumulation of data. As a result, certain views have been arrived at regarding the relations of the periods of particular flowers to particular species of insects, of families of plants to certain groups of insects, and the relative positions of different groups. Under these circumstances, Mr. Clarke's paper was read with particular interest, though it has not seemed to justify an abandonment of theoretical conclusions previously held.

The factors admitted by Mr. Clarke to have an influence in determining the blooming time of flowers are as follows:

1. "The blooming period may sometimes vary from the general rule to better bring the flowers among the most favorable conditions for cross-fertilization."

2. "Again, plants that are frontiersmen from the characteristic vegetation of a hotter clime may be expected in the hottest of the seasons—*e. g.*, the Cactaceae."

3. "There is an evident limitation of the flowering of our trees and shrubs to spring and earliest summer." "The blossoming of so many trees, especially the Diclinae, in earliest spring, before leaf-budding, must evidently have at least partial connection with anemophilous cross-fertilization."

4. "Again, there is a determining function in the character of the flower's habitat—the spring flowers seek largely the protection of the woodlands; marsh plants reach perfection mainly in latest spring and through the summer, though some, like Caltha, are early; the aquatics of ponds and river glory in the summer sun; and the flowers of meadow and prairie and thicket margin luxuriate from midsummer to the end of autumn."

But the principal deductions of Mr. Clarke are these: "*From early spring to late autumn there is a progression in the general character of the flower groups, from the lower to the higher—successive groups succeeding each other in time, parallel groups coming synchronously.* And the later in order may be *types* of a higher character of development, or they may be *specializations* of a group whose *normal* forms belonged to an earlier season. In their blooming season, *the more perfect succeed the more simple; the aberrant, the normal; the specialized, the generalized.*"

In the solution of the problem of the flower seasons of a given flora I think that the period of no plant should enter as a factor, if it is so far removed geographically that at its blooming time it does not become a competitor of any plant of that flora. Any number of flowers adapted to the same conditions may bloom at the same time if they are so widely separated that they do not interfere with one another, but it would be an obvious disadvantage for very many of them to bloom at the same time in the same locality. In the latter case a separation of the blooming times would be advantageous. On the other hand, there are some objections to the use of data derived from a local flora, though I think they are not so serious. Phenomena which seem to find an explanation in a limited field may in fact find their true explanation in conditions outside of that field. Even in the case of a local flora the time of blooming is likely to be indicated as too long, since it is based upon the early dates of early seasons, and the late dates of late ones. Such data give rise to error by making it appear that the period of an early species overlaps with that of a later one when in fact the two species never have flowers in bloom at the same time in any season. It is hardly practicable to avoid this, since observations confined to a single season are liable to be too fragmentary.

To note that a given family of plants is highly specialized and that it agrees with Mr. Clarke's generalization by reaching its maximum in summer, does not help one to understand either the general position of the family or the blooming time of a single species, and the difficulty remains the same whether the species blooms before or after the bulk of the family, or whether its season coincides with the maximum. The main fault that may be found with his elucidation of the subject is that it is implied that the general principle of the late blooming of highly specialized flowers is an explanation of the blooming phenomena; for, whenever a flower agrees with the generalization, it is left as if it were thus explained, while, if it is an exception, its period is accounted for under the considerations which we have numbered. And it must have been a striking fact to the readers of the paper that the exceptions yielded so readily to these considerations that they remained the only cases which were clearly elucidated. But it is hardly fair to dwell too strongly upon this point, for towards the close of the article, Mr. Clarke has expressly said: "Here the question rises, why should there be a correspondence between the course of the flower seasons and the system of floral evolution? Solve this and the 'Philosophy of flower seasons' is an open riddle." Stated in this way, as a very interesting and important fact to be explained, I see little in the paper to which objection can be made. Otherwise, it might not unfairly be considered as an attempted refutation of the Darwinian flower theory, for what becomes of that theory if it can be shown that the time of blooming of insect-pollinated flowers is not correlated with the time of flight of flower-loving insects?

The object of this paper will be to attempt a preliminary contribution to the subject from the standpoint of data derived from the *indigenous* local flora near Carlinville, Illinois (lat. 39° 21′), to test Mr. Clarke's main proposition, to undertake to account for flower seasons as a result of the competition of plants for the services of various pollinating agencies, and those of insect-loving flowers as also correlated with the flight of flower-loving insects, and to attempt an explanation of the fact of the general preponderance of the most highly specialized flowers in late summer.

When a plant in a plastic condition succeeds in establishing itself in a highly favorable position, it throws off a number of closely allied forms which finally become more or less well marked incipient species. As a result we find a number of nearly related forms in competition for a similar position in the soil, for a favorable position in the sunlight, and for the aid of the same pollinating agency. The process of producing similar forms may go on until the competition becomes so severe that it becomes disadvantageous. Then it becomes advantageous for some of the forms to avoid competition[1] with the dominant group by migrating to a different region, or to a different kind of soil, to modify their floral characters so as to attract a different set of visitors, or to separate their times of blooming so that they may not have to compete with a great many similar flowers for the attention of the same kinds of insects. As a consequence we find the forms separating their blooming times so as to come, some before, and some after, the maximum of the group, though the maximum of the whole will probably coincide with the position of the maximum of the dominant forms. The maximum point, then as a rule, at least, marks the point of origin of the group, but the struggle for existence requires a departure from it. Instead, therefore, of indicating a point of convergence for the group, the maximum point is the place of divergence, so that there is no law[2] according to which the forms tend to concentrate at this point. If one of the forms which has departed from the maximum point comes to fill a much more favorable position, it may finally give rise to so numerous a progeny of forms that the maximum of the group will change position and no longer coincide with the point of origin.

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[1] In the interaction of organisms in the struggle for existence it strikes me that a law of avoidance of competition is more obvious than that of the survival of the fittest.

In looking over my tabulations with these considerations in mind I note that, as a rule, incipient and closely allied species bloom synchronously, while more distinct species, and species of different genera are more likely to be widely separated. In large genera containing numerous closely allied species, which indicates a more recent origin, most of the species bloom together, and it is a notable fact that such genera have a potent influence in determining the maximum point of the groups to which they belong. Thus the species of buttercups (*Ranunculus*),violets (*Viola*), St. John's wort (*Hypericum*), tick-trefoil (*Desmodium*), golden-rods (*Solidago*), boneset (*Eupatorium*), sunflower (*Helianthus*), aster, milkweed (*Asclepias*), verbena, and smartweed (*Polygonum*), with rare exceptions, bloom simultaneously. The maximum of the buttercup family (Ranunculaceae) coincides with that of *Ranunculus*, that of Leguminosae with the position of *Desmodium*, while the maximum of Compositae is determined by the position of the asters, *Eupatorium*, golden-rods and sunflowers.

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[2] In the migration of some highly specialized groups which MacMillan calls "north bound," I think there has been a retardation of the blooming seasons which has tended to concentrate the species and thus form late maxima.

As a result of the divergence of the blooming periods from the maximum point of the group we find that plants come into competition with species of other groups, but as a rule they can stand this better than competition with their own allies.

Trees have such a remarkable influence upon one another and upon the herbaceous flora that they should properly, it seems, be considered separately. The fact that most of them agree in being wind-pollinated is an additional reason for this course. Of 488 indigenous insect-pollinated plants, upon which my observations are based, only 18 are trees. On examining the curve for the insect-loving flora (Fig 1, Plate VIII, 5 species to the millimetre),[3] it will be observed that the maximum is reached in August. At this time 187 species are in bloom, but not a single tree is among them. The flowers of trees are so interfered with by their own leaves and the leaves of other trees that it is disadvantageous for them to bloom after the leaves are fully developed. In the case of wind-pollinated trees it is obvious that, if the leaves were developed before the flowers, the process of pollination would be greatly impeded by the leaves interfering with the free circulation of the wind and catching the pollen which is intended for the stigmas. This fact makes trees an evident exception to Mr. Clarke's generalization, though they are frequently less specialized than their later flowering allies. In the anemophilous nettle family (Urticaceae) there is a marked contrast between the blooming times of the trees and herbaceous species, as stated by Mr. Clarke. Thus the elm, hackberry and mulberry are early, while the hop, hemp and wood-nettle (*Laportea*) are late.

In the case of insect-pollinated trees the conditions are similar to those of wind-pollinated ones, and they generally bloom before the leaves are developed, the witch-hazel notably after the leaves have fallen. The leaves act in an equally disadvantageous way, by concealing the flowers so that insects do not easily find them. Before the leaves have appeared in the woods, the trees which depend upon insects for pollination are very conspicuous and have a good chance of being attended by the insects which are attracted by their own flowers and by the flowers of the herbaceous plants which grow under their protection. Later, when the woods become shady, there are few herbaceous flowers, and few insects to attend the trees if they should bear flowers dependent upon them. The rose family (Rosaceae) is of particular interest, since of the larger families it contains the greatest number of trees., and as its maximum is early (Fig. 14, Plate VIII), it is the only one of the entomophilous tree-producing families, which is in a favorable position for giving rise to aborescent forms. The first to bloom is the service-berry (*Amelanchier*), and the trees, *e. g.*, the plum, cherry, apple and hawthorn, coincide pretty nearly with the maximum of the family, though it is significant that the latest species are herbaceous. As the season advances, the flowering of trees and of herbaceous plants which grow under them is evidently cut short in correlation with the appearance of the overshadowing leaves.[4]

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[3] Unless otherwise specified, the curves given in this paper are on the scale of one species to the millimetre, *i, e.*, the height of the curve in millimetres indicates the number of insects flying, or flowers in bloom at a given time. The details on which the curves are based will be given elsewhere.

While it is not my intention to discuss wind-pollinated plants specially at this time, I think that their blooming seasons may be explained by reference to their competition among themselves and with the insect-pollinated flora. Even in herbaceous plants it seems that the spring might reasonably be expected to be the most favorable for pollination, since they would be less likely to be overtopped by the later plants which become increasingly more luxuriant. But at different seasons they can readily occupy positions unfavorable to entomophilous plants, and in summer they may endure the competition of the entomophilous flora better than that of an indefinite number of plants depending upon the wind, or better than to resort to insect-pollination. In the cases of anemophilous Ranunculaceae, such as meadow-rue (*Thalictrum*), and Compositae, such as rag-weed (*Ambrosia*), it is probable that wind-pollination has been resorted to by way of avoiding competition with their allies, and it is notable that these plants bloom near the maximum points of the families to which they belong.

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[4] One of my favorite botanizing grounds shows a great variety of vernal flowers, but after the appearance of the leaves is covered by a uniform growth of the anemophilous wood-nettle (*Laportea canadensis*).

A comparison of the insect-pollinated Monocotyledons (Fig. 7, Plate VIII) with the general entomophilous flora (Fig. 1, Plate VIII) yields a more striking contrast than would result from a comparison of the two groups in general, for the former loses the large wind-loving families of sedges and grasses, the latter blooming late, and the general flora loses the early blooming wind-loving trees. In this group we observe that the terrestrial species, without regard to specialization, bloom early, while the aquatic ones are late. This I think is largely a result of the severe competition of the former with the highly specialized terrestrial flora, a competition from which the aquatics have been largely relieved by their position.

As regards those of the Liliiflorae having the carpels separate (apocarpal) and those having them united (syncarpal) I am unable to agree that the former are more highly specialized, and so must consider that their blooming time is opposed to the proposition that the more highly specialized flowers bloom later.

The curve for the Choripetalae (Polypetalae and Apetalae, Fig. 2, Plate VIII.—5 spp. per mm.) shows a maximum in August of 73 species, and a secondary maximum in April of 71 species, and the curve diminishes from both to about the middle of June, when there are 49 species in bloom. Of the Hypogynae (Fig. 3, Plate VIII.—2 spp. per mm.) 43 species bloom simultaneously in May, after which they pretty regularly decline. With the addition of the hypogynous Apetalae, the maximum remains the same, but there is a secondary elevation in August. The Perigynae (Fig. 5, Plate VIII. —2 spp. per mm.) show an August maximum on account of the strong preponderance of the Leguminosae. Among the

Epigynae (Fig. 4, Plate VIII) the ginsengs (Araliaceae), dogwoods (Cornaceae), wild ginger and pipe-vine (Aristolochiaceae), as Mr. Clarke observes, come early. In regard to the Umbelliferae (Fig. 18, Plate VIII), however, my observations do not show them "in fullest sovereignty in July and August," for at that time only four species bloom together, while there are 11 species in flower in May. Contrary to Mr.Clarke's theory, the more highly specialized Epigynae (Fig. 4, Plate VIII) show a stronger tendency than the Perigynae (Fig. 5, Plate VIII to form an early maximum.

Even the less specialized of the two dominant families of Perigynae (the Rosaceae, 14) does not equal the Umbelliferae in the formation of an early maximum, *i. e.*, it does not decline so rapidly from the early elevation. I think that the Umbelliferae are more highly specialized than the Myrtales (Lythraceae and Onagraceae) and so reverse the order of Mr. Clarke's theory. But the maximum of the Myrtales (17) anticipates that of the Leguminosae (15).

Of the hypogynous Sympetalae (Gamopetalae), the phloxes (Polemoniaceae), water-leaf family (Hydrophyllaceae) and borage family (Borraginaceae) are early; of 12 species all but one begin to bloom before June, and only two are in bloom after July 1st (Fig. 20, Plate VIII). The more numerous mint family (Labiatae, Fig. 13, Plate VIII) and Scropulariaceae (Fig. 19, Plate VIII) predominate in the summer. Observations on the Epigynae indicate that the flowers of the honeysuckle and madder families (Caprifoliaceae and Rubiaceae) are most abundant in the last of May and first of June. The lobelias and campanulas are most abundant in August. Of all the dominant families, the, Compositae (Fig. 21, Plate IX.—2 spp. per mm.) show the latest maximum. The tendency of the more highly specialized Sympetalae to form a strong late maximum is more marked than in the case of the more simple Choripetalae.

In order to illustrate to what extent the time of blooming of plants is correlated with the time of flight of insects, curves are reproduced showing the periods of the principal flower-loving insects, *e. g.*, the bees (Fig, 24, Plate IX), the other

Aculeate Hymenoptera (Fig. 25, Plate IX), the butterflies (Fig. 23, Plate IX), and the flies (Fig. 22, Plate IX)—all on the scale of five species to the millimetre. No curve is made out for the whole because these curves agree in showing a maximum for July, which, of course, would determine the position of the general maximum.[5] The bees are by far the most important, since they depend upon flowers both for their own food and for that of their young. As a rule, except in the case of the cuckoo bees, which lay their eggs upon food deposited by the host bees, the female bees are provided with brushes of hair upon which they carry pollen, the essential part of the bee-bread, upon which the larvæ feed.

In a previous examination of the curve for the Choripetalae (Fig. 2, Plate VIII) there was observed a maximum in August, a secondary elevation in May, and an intervening depression in June.

With the principal exception of the Leguminosae (Fig. 15, plate VIII), these plants have horizontally expanded regular flowers, with readily accessible nectar and stamens exposed so that the pollen is easily collected or eaten. The Leguminosae generally have lateral irregular flowers, with the nectar concealed and deep-seated, and intricately concealed pollen, for which reason they will be separated for special consideration. Now, since the maximum for the Choripetalae coincides with that of the Leguminosae, the separation of this family will change the maximum of the group to the secondary point. There are two families of insects which are particularly fond of simple flowers with easily accessible nectar and pollen—the less specialized bees (Andrenidae, Fig. 26, Plate IX.—2 spp. per mm.) and the flower-flies (Syrphidae, Fig. 36, Plate X.—2 spp. per mm.)—and they both have more species flying in early spring. There is no question but that the strong predominance of the more simple Choripetalae is, to a great extent, correlated with the early predominance of the Andrenidae and Syrphidae. The flowers of the buttercup family (Ranunculaceae, Fig. 9, Plate VIII) and of the Rosaceae (Fig.

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[5] My phaenological observations are most defective for August. I expect to find the maximum of the general anthophilous insect fauna a little later.

14, Plate VIII) with their numerous stamens are the particular favorites of the less specialized bees, and it would be fairly impossible for them to be so efficiently attended late in the season. No flowers are more convenient for the imperfectly adapted flower insects than those of the parsley family (Umbelliferae, Fig. 18, Plate VIII). While the later blooming species are visited by a more numerous set of insects, the visitors are less efficient. The flowers are somewhat neglected by the higher bees (Apidae, Fig. 27, Plate IX.—2 spp. per mm.). so that in order to secure the most useful set of visitors it is desirable to bloom early, under the maximum of the Andrenidae. I have shown that the harbinger of spring (Erigenia), the earliest spring flower, has a larger percentage of bees among its visitors than any other plant of the family, and that the early blooming species with simply concealed nectar show more bees as visitors than those with deep-seated nectar but blooming late. On consulting the curves for bees (24) and other Aculeate Hymenoptera (25) and flies (22), it will be observed that early in the season the predominant insects are bees and flies, so that by early blooming the less specialized flowers gain an advantage similar to that secured by the more highly specialized in a later season in concealing their nectar, *i. e.*, they acquire a higher proportion of the more efficient flower insects. The pond lilies (Nymphaeaceae) come in bloom late, probably on account of their aquatic habitat and have a long period, probably on account of occupying a position free from the competition of overshadowing form, but they are pollinated by late-flying bees and flower flies; and I have named two species of bees (*Halictus nelumbonis* and *Prosopis nelumbonis*) on account of their close economic relation to these flowers. The violets (Fig. 16, Plate VIII) are spring flowers, there being no normal late-blooming indigenous species. Those with the lateral petals bearded are adapted to the mason bees (Osmia, Fig. 31, Plate IX), small greenish species with pollen-collecting brushes on the ventral surface of the abdomen, which fly early apparently to avoid competition with the large allied genus of leaf-cutter bees (Megachile, Fig. 32, Plate IX). When visiting the violets these bees turn head downwards and hang upon the beards of the lateral petals while they collect the falling pollen. The violets also have an important pollinator in *Andrena violæ* of the spring group of *Andrena* (Fig. 35, Plate X). The swamp rose-mallow (*Hibiscus lasiocarpus*, Fig. 6a, Plate VIII) has a blooming time correlated with the time of flight of a characteristic American bee (*Emphor bombiformis*, Fig. 6b, Plate VIII), its principal pollinator; the bee in turn depending on the *Hibiscus* for its pollen. Another interesting case of correlation in appearance and mutual dependence is, that of an alum-root (*Heuchera hispida* Fig. 11a, Plate VIII) and a little bee (*Colletes aestivalis*, Fig. 11b, Plate VIII).

Returning to the Leguminosae (Fig. 15, Plate VIII) we observe that of the species which form the August maximum all are adapted to the most intelligent of the highest specialized genera of bees. Quite a number are bumble-bee flowers. The ordinary flowers have the stamens declined to the lower side and are best fitted to be pollinated by the leaf-cutter bees (Fig. 32, Plate IX), which have abdominal brushes for collecting pollen, and I think that the position of the family in general should be regarded as associated with the flight of these bees. Two species adapted to bumble-bees, a ground plum (*Astragalus mexicanus*) and a false indigo (*Baptisia leucophaea*), occur early, which they may do without going out of the range of bumble-bees (Fig. 30, Plate IX) and they each gain an advantage by avoiding competition with a late blooming congener also depending upon bumble-bees. But no other ordinary papilionaceous flower blooms out of the flying time of the leaf-cutter bees. The very earliest of the family, the red-bud (*Cercis canadensis*) has the stamens declined to the lower side of the flower, so that the pollen is easily gathered by the mason bees (Fig. 31, Plate IX), which we have already mentioned as having abdominal brushes, like the leaf-cutters (Fig. 32, Plate IX), but fly early. The early appearance of the red-bud seems to be influenced by the early flight of these bees, though it is not exclusively visited by them. Finally, therefore, with regard to the blooming phenomena of the Choripetalae, we close with the propositions that the early preponderance of the more simple open flowers is determined by the early predominance of the less specialized bees, and that the late preponderance of the more complicated closed flowers is correlated with the flight of the most specialized bees, leaf-cutters, bumble-bees, etc.[6]

The Sympetalae (Gamopetalae) consist of flowers with more or less deepseated nectar and often with closed complicated flowers. They are adapted to bumble-bees or to the more highly specialized bees in general, to butterflies or to miscellaneous more or less long-tongued insects. An interesting case is that of flowers of *Steironema* which are associated with the flight of *Macropis steironematis*, a bee which as far as observed depends exclusively upon these flowers for its pollen. The wild potato vine (*Ipomoea pandurata*) is dependent mainly upon two bees (*Entechnia taurea* and *Xenoglossa ipomoeae*). The flowers of ground cherry (*Physalis*) bloom during the flight of two species of *Colletes* (*C. willistonii* and *C. latitarsis*), upon which they depend almost exclusively for pollination, the little bees on the other hand, obtaining all of their pollen from these flowers. The dominant mint family (Labiatae, Fig. 13, Plate VIII) is principally adapted to the higher bees, although some having degraded irregular flowers with exposed stamens are adapted to miscellaneous insects. The figwort family (Scrophulariaceae, Fig. 19, Plate VIII) is an even more exclusive bee-flower family, most of them being adapted to bumble-bees, and appearing late. The earliest species, *Collinsia verna*, is one of the most highly specialized and looks like a papilionaceous flower. The upper lip and the lateral lobes of the lower lip represent banner and wings, while the middle lobe represents the keel, and it performs the same function for it contains the stamens, which instead of lying against the upper wall of the corolla, as is usual in the family, are declined across the tube. We have observed that most of the Leguminosae with declined stamens are adapted to bees with abdominal pollen brushes (*Megachile*, Fig. 32, Plate IX), and now in the case of this flower we find the principal visitors to be bees of the genus *Osmia* (Fig. 31, Plate IX); so that it joins the red-bud and violet in appearing during the flight of these bees. The figwort (*Scrophularia*) and *Symphoricarpus* come late in adjustment to the flight of the wasp workers and Eumenidae to which they are specially adapted. The late position of the lobelias is what might be expected, since they are dependent upon the visits of the higher bees (Fig. 27, Plate IX). We come finally to consider the great highly specialized family of sunflowers, nigger-heads, thistles, etc., (Compositae, Fig. 21,–2 spp. per mm. Plate IX) which shows a conspicuous late maximum and is the best example of Mr. Clarke's theory, though I think one of the easiest to explain without it.

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[6] The early blooming of the dominant families of Choripetalae, as well as the Liliiflorae, must also be explained in part as correlated with their woodland habitat, their decline being influenced by the appearance of the leaves on the trees.

The composite heads, which give the name to the family, are composed of florets arranged generally in a flat-topped horizontal layer which forms a convenient resting place for all kinds of insects. There is abundant nectar for the longer tongues and abundant pollen exposed for the least specialized to feed upon or to collect. From these peculiarities and from their great numbers we find this family to be of more importance to the general insect fauna than any other. The most important visitors are the higher bees, especially bumble-bees (Fig. 30, Plate IX), the leaf-cutters (Fig. 32, Plate IX) and *Melissodes* (Fig. 29, Plate IX), and lower Aculeate Hymenoptera in general (Fig. 25, Plate IX), the butterflies (Fig. 23, Plate IX), the flies, including many flower-flies (Fig. 36, Plate X), the tachinids (Fig. 37, Plate I), the conopids (Fig. 38, Plate X), and the bombylids (Fig. 39, Plate X). The occurrence of the maximum of the family after that of the general flower-loving insect fauna, I think, is largely due to the abundance of the golden-rods, asters, etc., which have rather small heads and less-deeply concealed nectar. The position of these flowers is accounted for in correlation with the position of the usually smaller insects by which they are attended, viz.; the little bees belonging to the genera *Calliopsis* (Fig. 34, Plate IX), the late *Colletes* (Fig. 33, Plate IX), the autumnal group of *Andrena* (Fig. 35, Plate X) and the Bombylidae (Fig. 39, Plate X)—all important guests and all having late maxima. These late Compositae have few competitors outside of their family and so are favorably situated, although the insect fauna has begun to decline. We will now leave the Sympetalae with the general statement that the late preponderance of the irregular flowers is explained in connection with the late preponderance of the higher bees, and that of the regular flowers is accounted for in the late maxima of the highly specialized long-tongued insects.

We have reviewed the principal groups of insect-pollinated plants and have noted a correspondence, more or less well marked, between their blooming seasons and the seasons of the insects upon which they depend. In different positions we find bumble-bee flowers and, although they all occur within the time of flight of these insects, it is not easy to explain why one of these flowers comes at one time and another at another time. Under the maximum of the buttercup family (Fig. 9, Plate VIII) we find a bumble-bee flower in the larkspur (*Delphinium tricorne*) and under the maximum of Leguminosae (Fig. 15, Plate VIII) another in a tick-trefoil (*Desmodium canadense*). We may say that the larkspur comes earlier because it had its origin in an earlier group. The flight of the bumble-bees, however, cannot be left out of consideration. It is obvious that a bumble-bee flower cannot arise at a time when the attentions of bumble-bees cannot be secured, so that the flight of the bees determines the time within which these flowers may have their origin. When a flower undergoing modification to suit bumble-bees changes its characters so that it no longer comes in competition with its allies, it becomes a competitor of other bumble-bee flowers. A point at which many of these are in bloom simultaneously would naturally be an unfavorable time, unless the new form should early offer more inviting attractions. If the blooming time were long, the attentions of the bees would be likely to be most constant at the point where there were the fewest competitors, and so finally the blooming time would tend to be limited to this point. Or if the earlier flowers were better tended, so that they became the most effectually fertilized, the blooming time would tend to become earlier. Some flowers we find far from the "tension" points of their groups, having no doubt shifted to take a more favorable position under the competition of other flowers. Thus the earliest member of the mint family (Fig. 13, Plate VIII), is a bumble-bee flower, and some of the earliest of the figwort family (Fig. 19, Plate VIII) are adapted to these insects. The larkspur itself is anticipated by four bumble-bee flowers belonging to more highly specialized families. We would, therefore, expect to find bumble-bee flowers at favorable points of origin or shifted to favorable positions, and the whole group of flowers so disposed as to share the services of these long-tongues with as little interference among themselves as possible. Of the sixty-four species on which the curve (Fig. 41, Plate X) is based the different forms succeed one another from the first of April until the middle of October in such a way that not more than twenty-five species are in bloom at the same time. Twenty-six have completed their flowering by the last of June. We will compare this curve with that for bumble-bees. The first bumble-bees which fly in the spring are the females; in May, June and July the workers appear; and finally in July, the males. The workers are more abundant and even more industrious than the females, and the males are frequently quite numerous and efficient flower visitors. In making a curve for bumble-bees (Fig. 30, Plate IX), therefore, I have introduced each sex as an element so that the maximum coincides with the flight of the three forms, and I think this is the only way to indicate in a curve the function of the genus as a pollinating agency. Now if we compare the curve for bumble-bees (Fig. 30, Plate IX) with the curve for the bumble-bee flowers (Fig. 41, Plate X) we find a well marked coincidence.

The curve for the other flowers adapted to the higher bees (Fig. 44, Plate X) indicates a more pronounced maximum, evidently because the higher bees in general show a more marked preponderance in summer. Of sixty-nine species on which the curve is based, thirty are in bloom simultaneously at the maximum point.

Now as observed above, the lower bees (Andrenidae, Fig. 26 Plate IX) prefer erect simple flowers with easily accessible nectar

PLATE VIII.

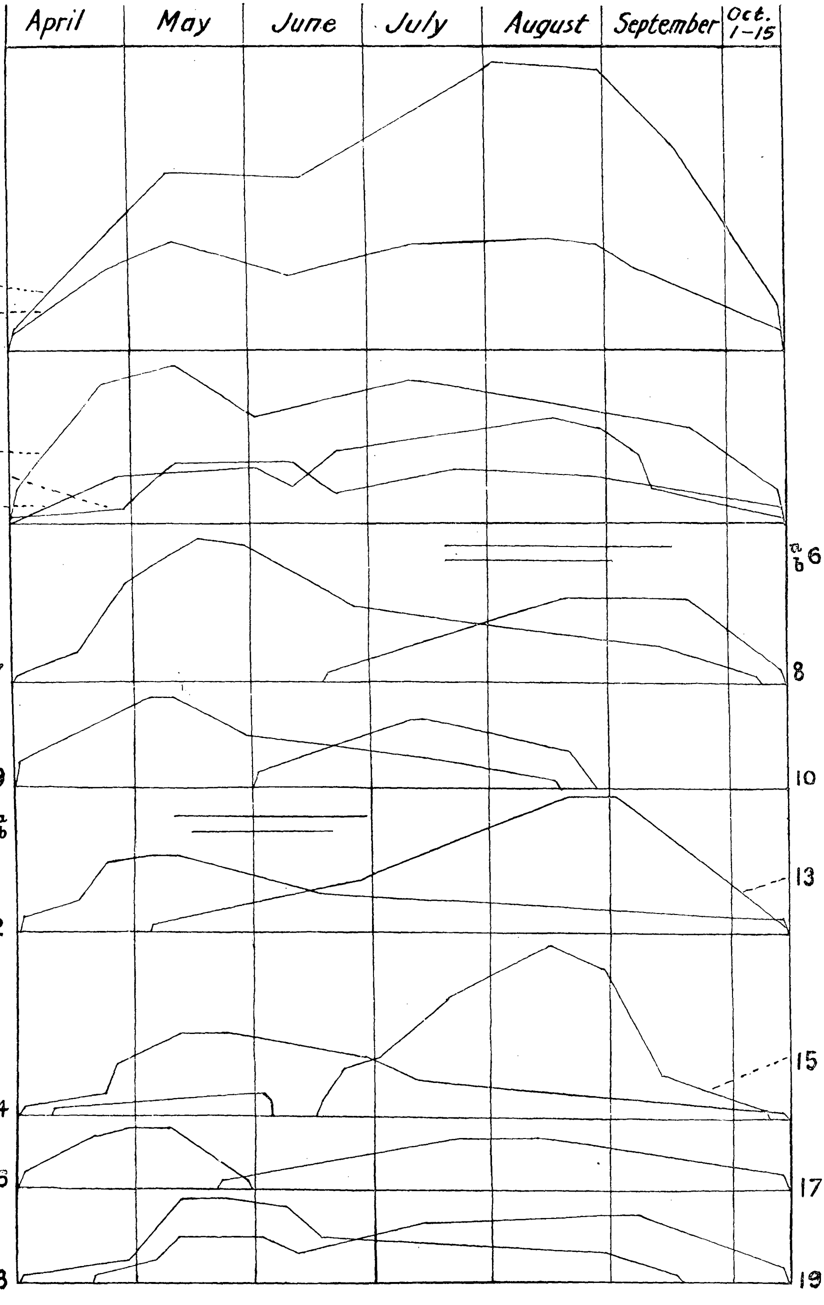
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PLATE IX.

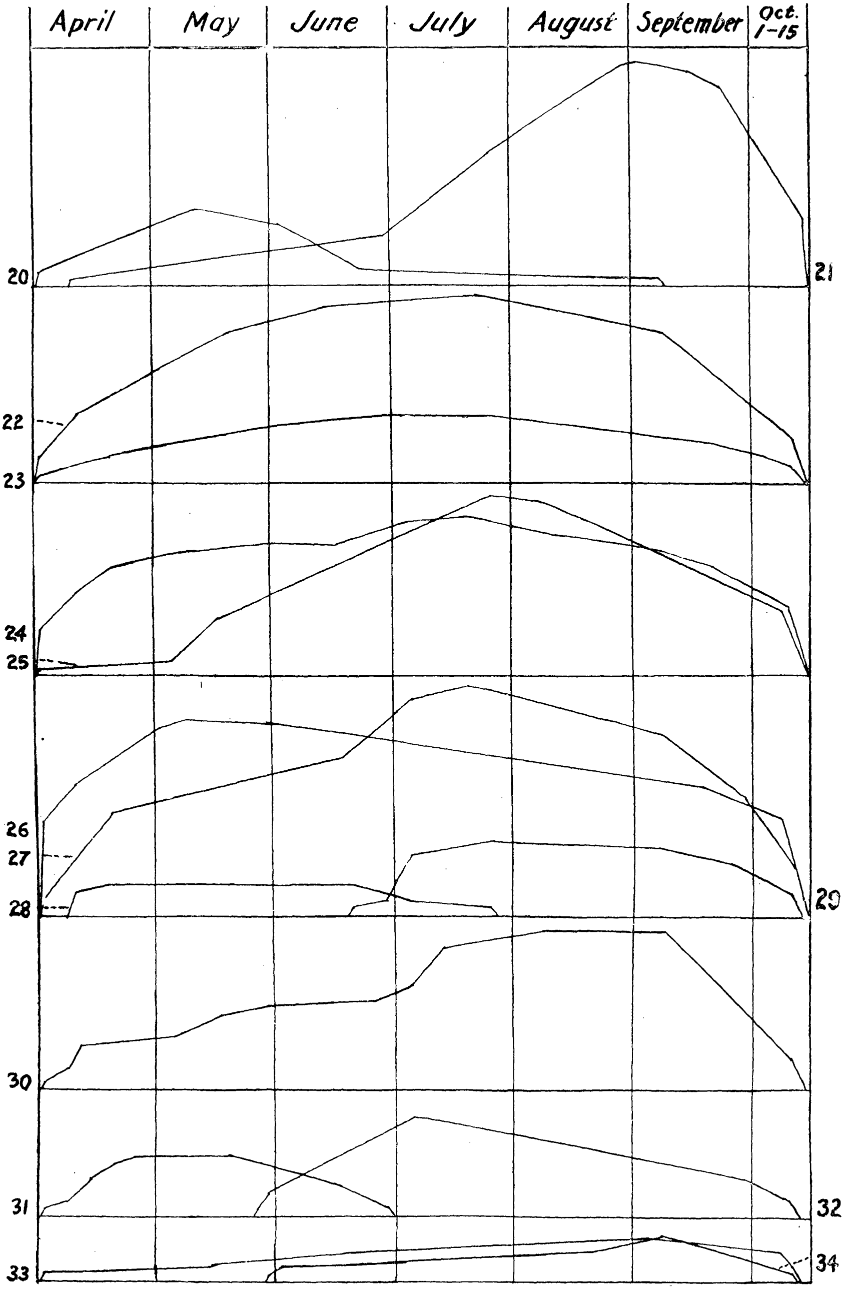
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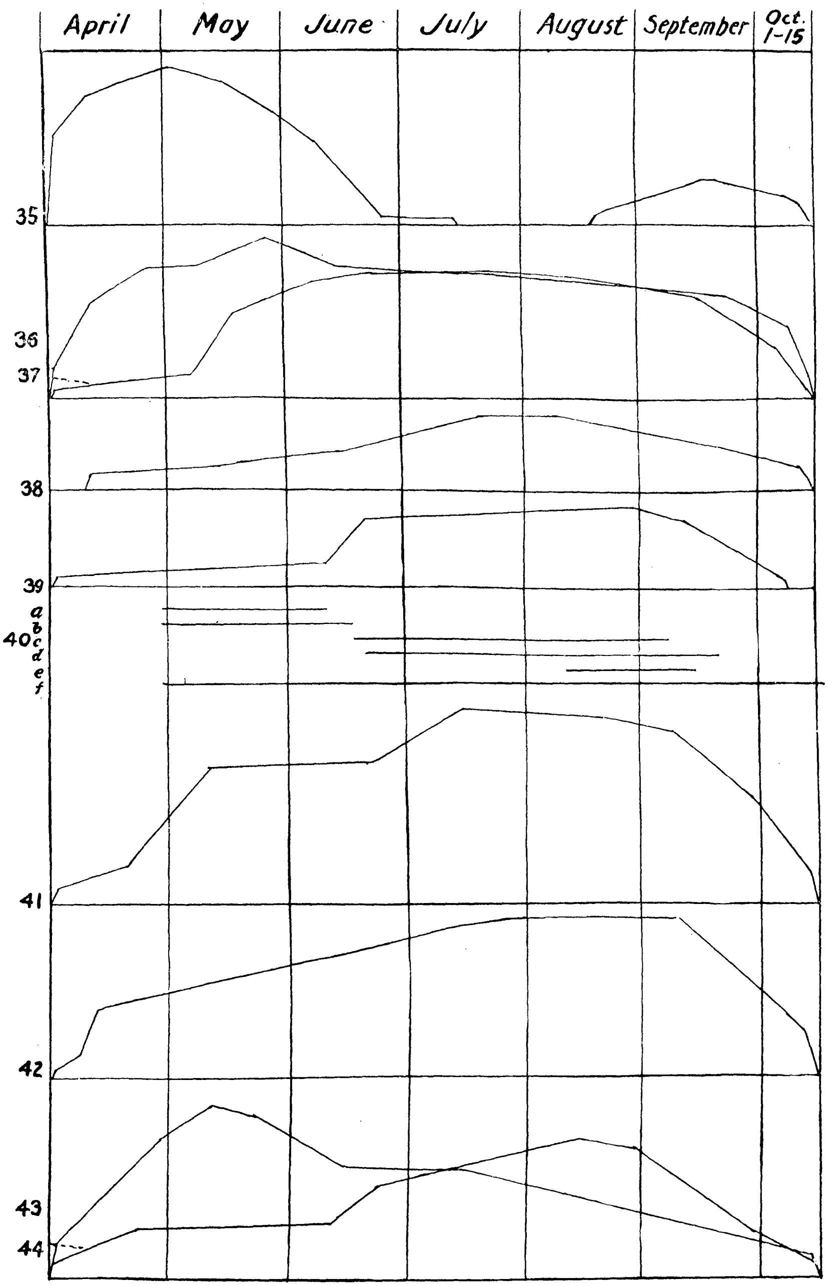
PLATE X.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and exposed pollen, especially flowers with numerous stamens. There are many flowers which have a structure of this kind and on which these bees actually preponderate over every other family of flower-loving insects. But since they do not hold a clear preponderance over the total of the other groups, it is hardly safe to call the flowers "Andrenid-flowers." The large family of flower-flies (Syrphidae, Fig. 36, Plate X) has the proboscis adapted for eating pollen and for sucking, though as a suctorial organ it is not so highly specialized as in many other flies. For this reason the flowers which are best fitted to supply the Andrenidae with nectar and pollen are also the most favorable for the nectar and pollen-eating Syrphidae, and when these two families are taken together they generally show a preponderance over all other visitors, or so many that the flower may be properly regarded as adapted to them. Putting such flowers together, I find that the *ensemble* of their blooming periods forms a curve like Fig. 43, Plate X, with a strong early maximum.

There are few evident butterfly-flowers. The best marked of them are commonly visited by long-tongued bees and flies. The species which are referred to this category form a long low curve, which we will compare with the curve for butterflies (Fig. 23, Plate IX).

Fig. 40, Plate X shows the time of flight of the ruby-throated humming bird (f) and the time of blooming of the flowers specially pollinated by it.—a. the painted cup (*Castilleia coccinea*); b. the wild columbine (*Aquilegia canadensis*); c. the trumpet creeper (*Tecoma radicans*); d. the spotted touch-me-not (*Impatiens fulva*); e. the cardinal flower (*Lobelia cardinalis*). There are two early species blooming together and going out about the time that the trumpet creeper (c) comes in, and three late species. The position of painted cup (a) is peculiar, but is much more favorable than in competition with the three late species. It will be noted that two species are in competition most of the time, while it is only a short time that one is alone or three are together. The spring and autumn migration of the bird may account for the tendency of these bird flowers to form an early and a late group.

The insects which contain what may properly be called flower-loving groups, viz.; the Hymenoptera, Diptera and Lepidoptera, are the most highly specialized orders of insects. The particular anthophilous groups we have observed to have their maxima in the late summer. With the exception of the bees, which are true flower-insects, depending upon flowers and showing true mutual correlations, the flight of these insects may be more properly regarded as determined by conditions favorable for their young. Flowers and flower-groups blooming at times favorable for utilizing them should be regarded as correlated with the time of flight of the insects, and not visa versa. Of the bees we have observed that the highest specialized (Apidae) show a late maximum while the less specialized (Andrenidae) show an early maximum, which is explained largely as a result of competition of the former. In view of the fact, therefore, that the most highly specialized flower-insects are most abundant in late summer it is but natural that there should also be a preponderance at the same time of the most highly specialized flowers whose development has been simultaneous with them. In so far as it applies to insect-pollinated flowers I think we have here the answer to Mr. Clarke's question " Why should there be a correspondence between the course of the flower seasons and the system of floral evolution ? "

We have observed that the group in which the fact of the correlation of a high specialization and late flowering is very conspicuous is the Sympetalae, and it must be admitted that the proposition of Mr. Clarke in regard to the late blooming of plants of southern derivation, must enter as an explanation. In his admirable work on the Metaspermae of the Minnesota Valley, Mr. MacMillan has shown that the Sympetalae (Metachlamydeae) are especially characterized by a north-bound movement.

Throughout this paper it has been implied that the time of blooming was determined by the flight of the pollinating insects and also determined and limited by the competition of plants one with another. In verification of this view turn to the case of introduced plants. It is well-known that introduced plants seem to flourish much more prosperously than the natives, and this is explained as owing to the fact that in a new country they escape the competition of forms which have been constantly undergoing modification to hold them in check. Many of our introduced plants, however, are not characterized so much by the facility with which they crowd out native species as by their habit of adjusting themselves to conditions induced by man, and of filling places rendered by him unoccupied; and in this work many of them no doubt have undergone a course of selective training in older lands. But it is sufficient for our purpose to start with the fact that introduced plants are to a great extent relieved from the pressure of competition which holds among the indigenous plants, and, therefore, as regards blooming, would be expected to flower longer. And this is in fact the rule. In those genera in which we have both indigenous and introduced species the former bloom for a short time (*Sisymbrium canescens, Stellaria longifolia, Cerastium nutans*, sunflowers, thistles) while their introduced congeners bloom much longer (*Sisymbrium officinale, Stellaria media, Cerastium vulgatum, Helianthus annuus, Cnicus lanceolatus*). The introduced species of Cruciferae, Caryophyllaceae, Portulacaceae, Malvaceae, Leguminosae, Umbelliferae, Compositae, Scrophulariaceae, Labiatae and Polygonaceae present cases of long blooming which are not equaled by any native species of the respective families.

Some native plants which have a strong tendency to occupy waste grounds also show a tendency to bloom for a long time. A similar disposition is manifested in the cases of plants having small flowers infrequently visited by insects and often self-pollinating. Many originally aquatic plants and others which have been forced to take to the water are, like introduced plants and the degraded entomophilous flowers, relieved from the severer competition of terrestrial plants and in a similar way show a tendency to prolong their blooming periods.

In the case of the indigenons flora there is a well marked disposition to limit the blooming period in anticipation of the advancing winter. The direct effect of cold is not obvious, but there is an evident tendency not to prolong the period until the conditions should become unfavorable for the perfection of the fruit. In the case of the north bound groups (Sympetalae especially) we might infer that the northward movement would retard the blooming time so as to make it later in beginning, and to prolong it far into the autumn. I have thought that this might have something to do with the late preponderance of these groups. The curves for Labiatae (Fig. 13, Plate VIII) Compositae (Fig. 21, Plate IX) and Leguminosae (Fig. 15, Plate VIII) seem to show the influence of the approaching cold to an unusual degree, for they fall off quite suddenly from the late maxima. In the case of introduced plants we have observed that they show in a low degree the limitations which beset the indigenous species and so tend to prolong their periods. The advancing winter brings conditions, however, which they cannot escape, and it is but natural that they should show the direct effect of cold more than the indigenous plants. They form a low curve which is relatively higher at the 15th of October than any other curve. Although only about one-tenth of the entomophilous species, the introduced species show two-fifths of the flowers in bloom at the middle of October. Their blooming time is actually cut short by the cold.

An interesting fact in regard to the curves for the dominant groups of flowers is that they decline towards June. In the curves for the general flora and the Choripetalae and its groups (1–5) it will also be observed that there is a depression in June. The same occurs in Scrophulariaceae (Fig. 19, Plate VIII), while the Leguminosae (Fig. 15, Plate VIII) show an actual gap, as far as I have observed. This results mainly I think from the appearance of the dense shade in the woodlands, which limits the blooming seasons of the vernal woodland species. No plant can become a strong competitor of the vernal species unless it blooms early enough to fill out its season before the shade appears. The late species are thus required to modify their seasons so greatly before they are prepared to enter the vernal woodlands that the trees finally become as effectual a barrier against them as against the late blooming of the early species. Suppose that the Compositae should give rise to an early flowering group which should enter the woodlands and become competitors of the spring flora, as *Antennaria* and some species of *Erigeron* now do. The curve for Compositae would finally show a June depression. These conditions must always keep the groups from taking the positions required by Mr. Clarke's theory.